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GENETIC EVIDENCE OF ALLOPARENTAL CARE OF A FEMALE LESSER KESTREL IN AN ALIEN NEST

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Care of nondescendant young (alloparental care) is relatively common in many bird species (Reidman 1982, Skutch 1987). In most cases, alloparental behavior occurs either when nonbreeding birds care for offspring that are not their own or when reproductive adults adopt or feed young that are not their own. Provisioning of food by birds other than the parents is expected more frequently in communal species because of the increased chance of exposure of nonbreeding individuals to hungry nestlings (Jamieson 1989) and also because of the chance of amalgamation of nestlings among contiguous nests (Cooper and Miller 1992). In any case, alloparental care poses a nonresolved question on its possible adaptive significance (Jamieson 1989, 1991, White et al. 1991, Ligon and Stacey 1991, Emlen et al. 1991).

The Lesser Kestrel (*Falco naumanni*) is a colonial falconiform in which adoption has been reported (Donázar et al. 1991). This behavior may occur at high frequencies in certain populations when nest-site densities are manipulated, and when nestlings are able to move to alien nests, where they may benefit from alloparental feeding (but see Tella et al. 1997). Adoptions like this could be actively sought by nestlings in species in which adults show no apparent ability to discriminate between their own and alien young (Tella et al. 1997). In this colonial species there has also been one case reported in which two females mated polygynously with the same male and laid eggs in one nest, though only one female attended the mixed brood and provided alloparental care to the unrelated young (Tella et al. 1996). In this paper, how-

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Table 1. Independent band-sharing coefficients of two neighboring families of Lesser Kestrels. F1 was the adult female breeding at nest 1; M1 was the adult male breeding at nest 1; F2 was the first-year female of nest 2 that also provisioned at nest 1; O11–O14 were offspring from nest 1; O21–O22 were offspring from nest 2. Mean number of bands scored = 17.8 ± 1.7 (SD; $N = 9$).

	F1	M1	O11	O12	O13	O14	F2	O21	O22
F1	—	0.2	0.4	0.4	0.5	0.4	0.2	0.1	0.1
M1		—	0.7	0.6	0.7	0.6	0.2	0.1	0.2
F2			0.2	0.2	0.2	0.2	—	0.4	0.5

ever, we describe and analyze through DNA multilocus fingerprinting, a different kind of alloparental care in which a breeding female provisioned food in two different nests: her own and an alien nest in the colony.

STUDY AREA AND METHODS

Lesser Kestrels form breeding colonies in abandoned field houses and nests are usually under tiled roofs or inside holes in the walls. The colony under study consisted of 27 breeding pairs and was located in the tiled roofs of an abandoned farm of La Mancha (Ciudad Real, Spain). Aparicio (1997) provides more details about the study area.

Nest sites were located before the onset of laying by watching mated pairs. Each potential nest was monitored every 4 d from 20 April to find the first eggs and then every 2 d until the clutch was finished. Eggs were labeled with a water-proof, felt-tip pen. Adult kestrels were caught and marked with a unique combination of colored and metal rings. At hatching, each chick was marked with a felt-tip pen or with nail varnish on the nape, back or wings, and they were also banded with metallic rings at the age of 6–7 d. Parental feeding rate was routinely recorded either by direct observation or with a video camera for 30 min at each nest every 5 d. Two nests were involved in this study: nest 1 (N1) that contained the chicks of adult pair 1 (P1) and nest 2 (N2), 3.5 m apart that was attended by a 1-yr-old pair (P2), a male in first-year plumage and a female (F2) ringed the previous season as fledging. The female (F1) from N1 had bred for several years in the colony, whereas the male (M1) was in full-adult plumage and was unringed. No other occupied nest was located between the mentioned nests, although two more pairs nested in that particular roof of the farm. The 1-yr-old female (F2) also provisioned food to offspring of N1. Intraspecific brood parasitism has been recorded in the Lesser Kestrel (Negro et al. 1996). To detect possible cases of brood parasitism which could explain the behavior of F2 provisioning N1 offspring, both adults from N1 and the female from N2 were trapped with a noose carpet trap and blood samples were collected; we could not capture the first-year male from N2. We extracted DNA from blood samples of the three adults and their respective attended nestlings and analyzed for parentage using Jeffreys' derivate pSPT 18.15, following a standard protocol for DNA-multilocus fingerprinting (Wetton et al. 1987). All results given are mean ±SD.

RESULTS AND DISCUSSION

During the recording of parental feeding rates in 1997, alloparental care was detected three times during 30 min of observation at N1, located in an area of the roof with only two occupied nests. However, no instance of feeding by F2 at her own nest (N2) was detected during this time When the observations occurred, the offspring of the receiver nest (N1) consisted of four chicks, 20-d-old, attended by P1 and F2 of N2. N2 contained two 17-d-old chicks, fed by both parents. N1 later produced four fledglings with a mean mass of 145 g and N2 two fledglings with a mean mass of 129.5 g (mean fledgling mass in the colony = 133.4 ± 11.6, $N = 21$ nests measured at 30–35 d). Feeding rates per hr and per nestling were similar at N1 (5 ± 2.6 deliveries by the male and 3.7 ± 2.1 by the female) and at N2 (4.9 ± 5.9 by the male and 2.4 ± 4 5 by the female), (males: $t = 0.04$, df = 12, $P = 0.97$; females: $t = 0.7$, df = 12, $P = 0.5$; males and females: $t = 0.65$, df = 12, $P = 0.52$).

Adults attending N1 were the genetic parents of the complete brood, although band sharing was not the same for the father (0.68 ± 0.02) and the mother (0.46 ± 0.04, paired $t = 13.5$, df = 3, $P < 0.001$; Table 1). Also, F2 attending N2 was the genetic mother of her attended offspring. The mean proportion of band sharing of presumptive first-degree relatives was 0.55 ± 0.12 ($N = 10$) and the mean for the presumed unrelated individuals was 0.21 ± 0.04 ($N = 11$); this latter value was consistent with the background band-sharing coefficient for a distinct population of the same species using a different probe (Negro et al. 1996). Young from N2 were unrelated to the adults of N1 (band-sharing coefficients of 0.13–0.27 and 8–9 novel bands were absent in F1 and M1) and F2 had no apparent genetic relationship with P1 or the young of N1 (Table 1). Based on total number of bands and number of bands shared, and assuming a band sharing of 50% for first-degree relatives, we calculated the binomial probability for two individuals to be first-degree relatives. We estimated that the probability of F2 being a first-degree relative with F1 was 0.018 and the probability that F2 was a first-degree relative with M1 was 0.005. The combined probability of F2 being a first-degree relative with either F1 or M1 was 0.02. These estimates do not

discard a second-degree relationship between F2 and either F1 or M1 although, in such a case, kin recognition among breeding individuals should not be expected in a species in which parents do not seem to recognize their own offspring (Tella et al. 1997, J. Aparicio unpubl. data). For this reason we discard that kin relationships were responsible for the behavior described here.

The analysis of DNA multilocus fingerprinting also precluded the possibility of intraspecific brood parasitism and potential switching of the chicks in the nests. This was also supported by field observations as the female from N1 started laying eggs two days before the female at N2. Further, the laying intervals were uniform and clutch size in both nests was five eggs, a large value in a population in which clutches of six are very rare (0.9%). Also, nestlings were ringed at a very early age (6–7 d) and it was unlikely that they moved to the other nest before ringing because this behavior occurs, on average, at 25 d (Tella et al. 1997).

Other possible explanations for the alloparental care observed were mistaken identity, reciprocal altruism, or manipulation of the adults by the chicks (e.g., Birkhead and Nettleship 1984). Mistaken identity may be a source of nonadaptive provisioning to nonrelated broods. However, because of the distance of the two nests (3.5 m) and their different positions (N1 was by the edge of the roof whereas N2 was central, and there was a garret exit of 1 5 × 0.8 m and a chimney separating them), a location mistake seems unlikely even though we do not know the precise cues used by adult Lesser Kestrels to locate their nests. Also, we did not detect reciprocal altruism during the observations; however, this possibility could not be discarded altogether. Adults from N1 provisioning N2 chicks could have gone unnoticed during our observations.

We do not know how rare this behavior might be. In fact, during more than 10 yr of study of several breeding colonies (e.g., Aparicio and Cordero 2001, Aparicio and Bonal 2002), this behavior was detected only when systematic observations were made at a few nests for another purpose. In a species, in which adoption may be relatively frequent and adults do not recognize alien offspring as in the Lesser Kestrel (Tella et al. 1997, J. Aparicio unpubl. data), begging may be a strong stimulus promoting alloparental care, particularly if the cost of infrequent provisioning is negligible (Pierotti and Murphy 1987). Nestlings from N1 were larger than those of N2 and begged for food more frequently and more vigorously, displaying their beggings by putting their heads out of the nest whereas chicks from N2 did not when the alloparental behavior occurred. Nevertheless, the differences in mass, feeding rates, and incubation length obtained for N1 and N2 may be more attributable to individual differences of the parents (i.e., because of age) rather than to observed alloparental behavior. This may be particularly so in the exceptionally good year of 1997 in which prey were extraordinarily abundant, which diminishes the cost of foraging (J. Aparicio unpubl. data) Our results suggest that in the absence of kin selection, a more parsimonious mechanism for the alloparental care described here may be an irresistible response to food begging and gaping (Jamieson 1989). Thus, under certain circumstances, nestlings may manipulate alloparental care by begging, especially care from inexperienced females, even from their own nests.

RESUMEN.—El cernícalo primilla es una especie que nidifica en densas colonias en construcciones humanas. En esta especie es conocida la conducta aloparental cuando los pollos de cierta edad pueden moverse hasta otros nidos donde se camuflan entre los pollos del mismo y son alimentados por adultos no emparentados genéticamente con ellos. Aquí describimos una conducta diferente de cuidado aloparental, de una hembra de primer año alimentando pollos en dos nidos, uno propio y otro ajeno. Los análisis de DNA multilocus fingerprinting revelan que no existe parentesco genético entre dicha hembra y los pollos o los adultos del nido ajeno. Se revisan las distintas hipótesis que pueden explicar este caso de cuidado aloparental. Se sugire que bajo ciertas circunstancias, los pollos pueden manipular el cuidado aloparental incluso desde sus propios nidos.

[Traducción de los autores]

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NESTING OF LONG-EARED OWLS ALONG THE LOWER BIG LOST RIVER, IDAHO: A COMPARISON OF 1975–76 AND 1996–97

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KEY WORDS: *Long-eared Owl*; Asio otus; *nesting*; *riparian*; *Idaho*.

Long-eared Owls (*Asio otus*) are found throughout much of North America and Eurasia, typically inhabiting open forests or dense vegetation adjacent to open grasslands or shrublands (Marks et al. 1994). These owls generally nest in abandoned stick nests of other birds. Research from 1975–76 (Craig 1977, 1979, Craig and Trost 1979) provided information on Long-eared Owls that nested along a 25-km stretch of the Big Lost River on the Idaho National Engineering and Environmental Laboratory (INEEL) in southeastern Idaho (Fig. 1). These nesting Long-eared Owls used abandoned Black-billed Magpie (*Pica pica*) nests built in narrow-leaved cottonwood (*Populus angustifolia*) trees.

Diversion of water for irrigation, the INEEL flood control diversion dam, and recent droughts have dewatered the Big Lost River during much of the summer, contributing to the decline of narrow-leaved cottonwood trees growing on its banks. The INEEL diversion dam was constructed in 1958, and the dam and containment dikes were enlarged in 1984 to reduce the threat of floods to research facilities on the INEEL (Stone et al. 1993). Annual flow records from 1965–98 for the Big Lost River on the INEEL (at Lincoln Boulevard Bridge) vary greatly but demonstrate a general decline in stream flow and two multi-year periods of zero or nearly zero stream flow (Fig 2). The periods from 1977–80 and 1987–94 were partic-

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